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Surface Molting Behavior and its Possible Respiratory Significance for a Giant Water Bug

Abedus herberti Hidalgo

(Hemiptera: Belostomatidae)

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Relatively little attention has been given insect molting behavior. Entomological textbooks (*e.g.* Borror and DeLong 1971, Romoser 1973, Ross 1965) usually accompany their discussion of the protective qualities of the integument with assertions of the vulnerability of insects during their molts. These discussions invariably neglect to suggest how insects behave in ways to minimize risks and to meet other challenges presented by the necessity to molt. Wigglesworth (1972) reviews the literature on the physiology of molting, stressing the function of ingested air or water in swelling the thorax to cause the initial integumentary rupture. He does not mention the importance of substrate in this context, but other authors (Snodgrass 1919, Corbet 1957) suggest that adequate substrate is a requisite for the molting of some insects, with the implication that contractions of thoracic musculature associated with the legs may be necessary to initiate ecdysis.

Respiration presents a special challenge in the molting of aquatic Hemiptera. The majority of nymphs of totally aquatic bugs (Hydrocorisae) utilize an air film for underwater respiration. Air is obtained from the atmosphere at the air-water interface and maintained on the body of the insect by means of hydrofuge pubescence. Since this air store is integral with the integument, it is effectively, if not actually, lost shortly after the onset of shedding. Hungerford (1920) reviews the literature on the biology and ecology of aquatic Hemiptera, but fails to mention molting behavior. In his notes on the last molt of *Lethocerus americanus* Say, Torre Bueno (1924) stated that this insect floats "with its back up" during the molting process. Menke (1960) observed that *Abedus* nymphs shed "while the bug is floating, legs spread, at the

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surface." Tawfik (1969) seems to be the first to have speculated on the adaptive significance of surface molting by a belostomatid. He stated that in *Lethocerus niloticus* Stål (= *Lethocerus cordofanus* Mayr), "The functional abdominal spiracles, which are located dorsally on the adult, are situated ventrally on the nymph's body. For this reason the mature nymph, in the act of molting, becomes anxious to keep the thorax over the water surface and thus the thoracic spiracles become (sic) in contact with atmospheric air." Some of Tawfik's ideas on respiratory morphology, presumably taken from Presswalla and George (1935) are in error, and he fails to mention the behavior of nymphs in molting prior to the definitive molt. It is also unclear from his statements why it would be important to keep the thoracic spiracles in contact with air if the abdominal spiracles are the functional ones, but I agree that surface molting must in some way function to provide for the respiratory needs of the emerging nymph or imago.

It is my purpose in this paper to recount in detail the molting behavior of *Abedus herberti* Hidalgo, to point out certain neglected aspects, and to discuss ways in which surface molting may function to provide for respiratory needs of the molting individual.

METHODS AND MATERIALS

In the genus *Abedus*, females lay their eggs on the back of the male. I obtained first instar nymphs from egg-encumbered male *Abedus herberti* collected in central Arizona. Laboratory rearing of 31 individuals provided ample opportunity to observe numerous molts of all instars. No less than three molts of each instar were observed. I used still and motion picture photography to record events for detailed study. My rearing techniques are detailed in another paper (Smith 1974).

MOLTING BEHAVIOR

The following account is a synthesis of my observations on the molting behavior of first through fifth instars. Since the description is keyed to Figure 1, the final molt is emphasized.

One to five days prior to the onset of actual shedding of the old skin, the integument begins to darken. This signals the separation of the old integument from the new. In later instars the wing pads show a reddish reticulate pattern; this is especially pronounced in the fifth instar. The day before a molt is to occur, the abdomen and to a lesser extent the thorax and wing pads take on a deep brownish-orange color. Dark black triangles appear on the visible portion of each side of the

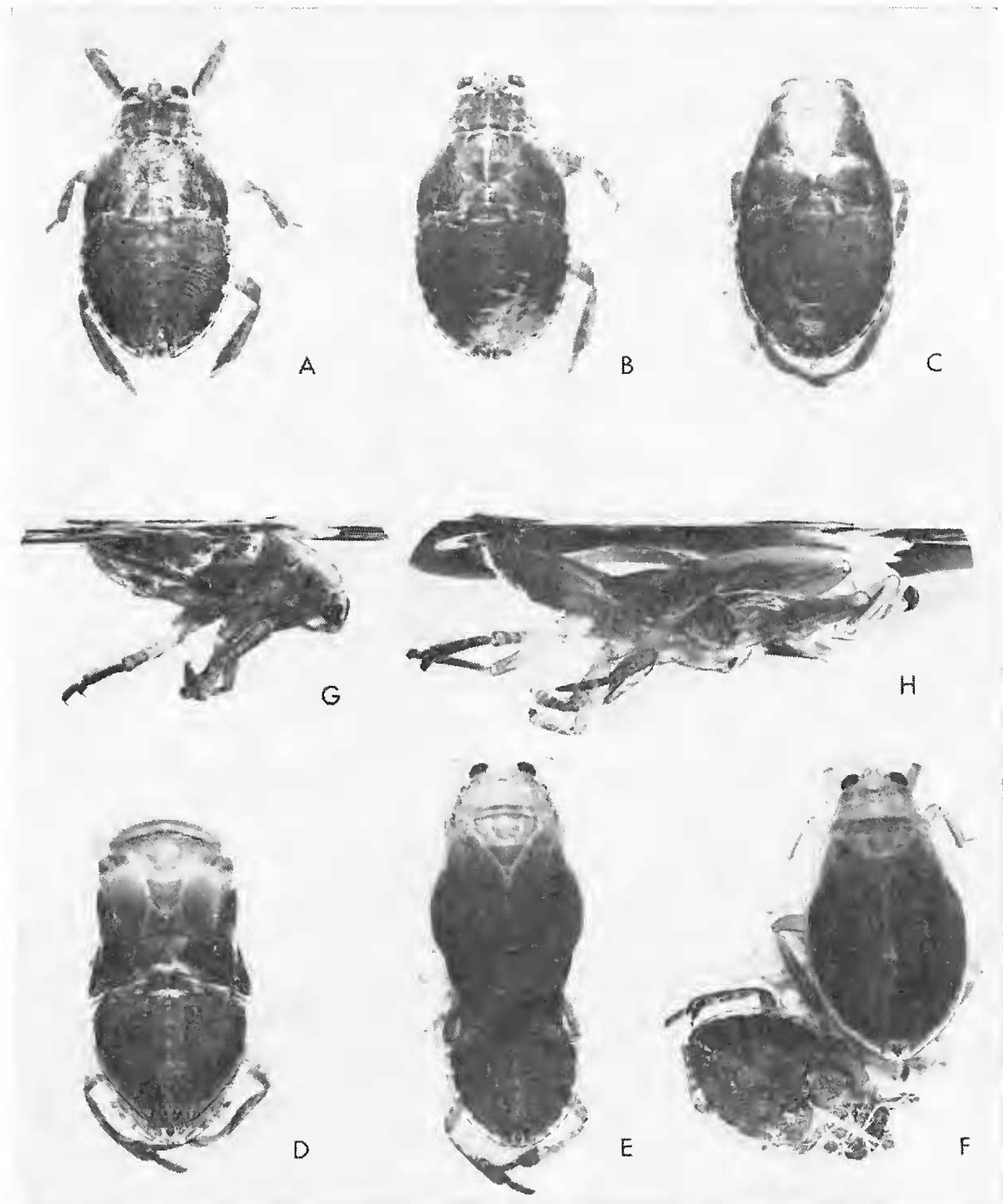


FIG. 1. Final molt of *Abedus herberti*. A through F: Dorsal aspects of the molt sequence. G: Lateral view equivalent to C. H: Lateral view equivalent to E.

metatergum, with the base of each adjacent to the wing pads, and its apex pointing toward the midline. Nymphs ignore food at this time, and remain floating at the surface continuously.

Dorso-ventral thickening occurs noticeably on the day of the molt, and actual ecdysis begins with the distention of the head away from the prothorax and the prothorax from the mesothorax (Fig. 1A). This seems the point of no return, although an individual can still swim

awkwardly if disturbed. No amount of disturbance, however, can long delay the following process which proceeds at the discretion of the bug. In all of the more than 15 molts I observed, the nymph initiated integumentary rupture by grasping its mesotibia with its raptorial protibia (Figs. 1B, 1G, and 2). This causes the thorax to arch and the resulting pressure immediately ruptures the integument (Fig. 2) along the middorsal (ecdysial) line beginning at the juncture of the pro- and mesotergum and proceeding posteriorly to the juncture of the meso- and metatergum. At this point the bug begins bending its head ventrally, continuing the integumentary split anteriorly into the coronal and laterally into the frontal ecdysial sutures of the head (Figs. 1C, 1G, and 2). Abdominal peristaltic-like contractions cause lateral separation of the meso-metatergal suture to the wing pads or lateral margin, leaving the conjunctival membranes intact. Shortly following, the metatergal, first abdominal-tergal junction is separated on both sides of the split, as the middorsal split lengthens through the metathorax into the scutellum. At about this time the head and prothorax are freed from the old skin. Contractions continue, and in the case of the emerging adult, the wings are inflated as they are withdrawn from their pads (Fig. 1D). It is noteworthy that at some time between the conditions illustrated in Figure 1C and Figure 1D, the silvery ventral abdominal air store is lost. When the bug is two-thirds free of its old skin, it flattens its body (in relation to the water's surface), extracting the legs which are brought forward, folded and nested at the sides of the pronotum (Fig. 1E and 1H). The individual usually rests in this position for from one to 20 minutes. Several quick thrusts with the hind legs complete the molt, leaving the exuvia floating and streaming its white tracheal linings (Fig. 1F). At this time the adult's wings are completely inflated and the hemelytra locked together. Newly molted instars and imagoes are light yellow in color. Pigment development and cuticular hardening required from one hour in the case of a second instar to eight hours for an adult. A newly emerged nymph or imago quickly acquires a new air store by breaking the surface film with its abdominal apex or air straps, and then generally spends some time grooming its beak with the forelegs and respiratory organs (abdominal air-retaining pubescence and/or air straps) with the hind legs preparatory to assuming a predatory stance below the surface.

Molting in the laboratory occurred throughout the day. In the field, I observed four individuals molting; two of these occurred at night and two during the day.

SURFACE MOLTING AND RESPIRATION

Molting on the surface of the water would seem to be disadvantageous for several reasons: the surface-molting individual is exposed to predation from above and below; it fails to take advantage of available cover (plants, debris, etc.) occurring below the surface; and it is deprived of a substantial substrate to facilitate integumentary rupture. Why then has this behavior evolved? The easiest explanation is that surface molting places the emerging nymph or imago in proximity to its primary source of oxygen, *i.e.* the air-water interface. This is not, however, an entirely satisfactory explanation. *Abedus* usually lives in quiet water of shallow streams where a swim to the surface for the first "breath" of air after a molt would not seem overly taxing. An alternative hypothesis is that the respiratory requirements of the pre-molting or molting nymph preclude subsurface ecdysis.

Dr. Margaret Parsons has offered (*in letteris*) some tentative ideas on how respiration may occur during surface molting. The reader should take care to note that Dr. Parsons' interpretations are based only on her study of Figure 1 against the background of her investigations of respiratory morphology in aquatic Hemiptera including *Belostoma flumineum* (1972a, 1972b, 1973). Her interpretations and underlying assumptions follow in this paragraph: Assuming (1) that *Belostoma* and *Abedus* are essentially similar in respiratory behavior of both nymphs and adults, and (2) that spiracular function is much the same in both genera (*i.e.* the first abdominal spiracles are the main inhalant pair for both), the problem for the nymph is to keep the first abdominal spiracle in contact with a source of oxygen prior to and perhaps during the time it takes to shed the nymphal cuticle. To do so, this main inhalant spiracle must be kept in contact with atmospheric air. Figure 1G shows the fifth instar with its posterior end and dorsal surface in contact with the water's surface. In this position atmospheric oxygen can reach the first abdominal spiracle by way of the ventral abdominal air store (ventral bands of hydrofuge pubescence), which communicates posteriorly with the atmosphere. This enables the bug to inhale atmospheric oxygen until the stage shown in Figure 1D and 1H. Here the posterior end of the body is submerged and as previously noted, the ventral abdominal air store has disappeared. Perhaps the adult (nymphal) first abdominal spiracle is able to inhale air from the cast-off nymphal skin, since there appears to be no other obvious source of oxygen communicating with these inhalant spiracles at this stage in the molt. (The duration of the rest period previously referred to,

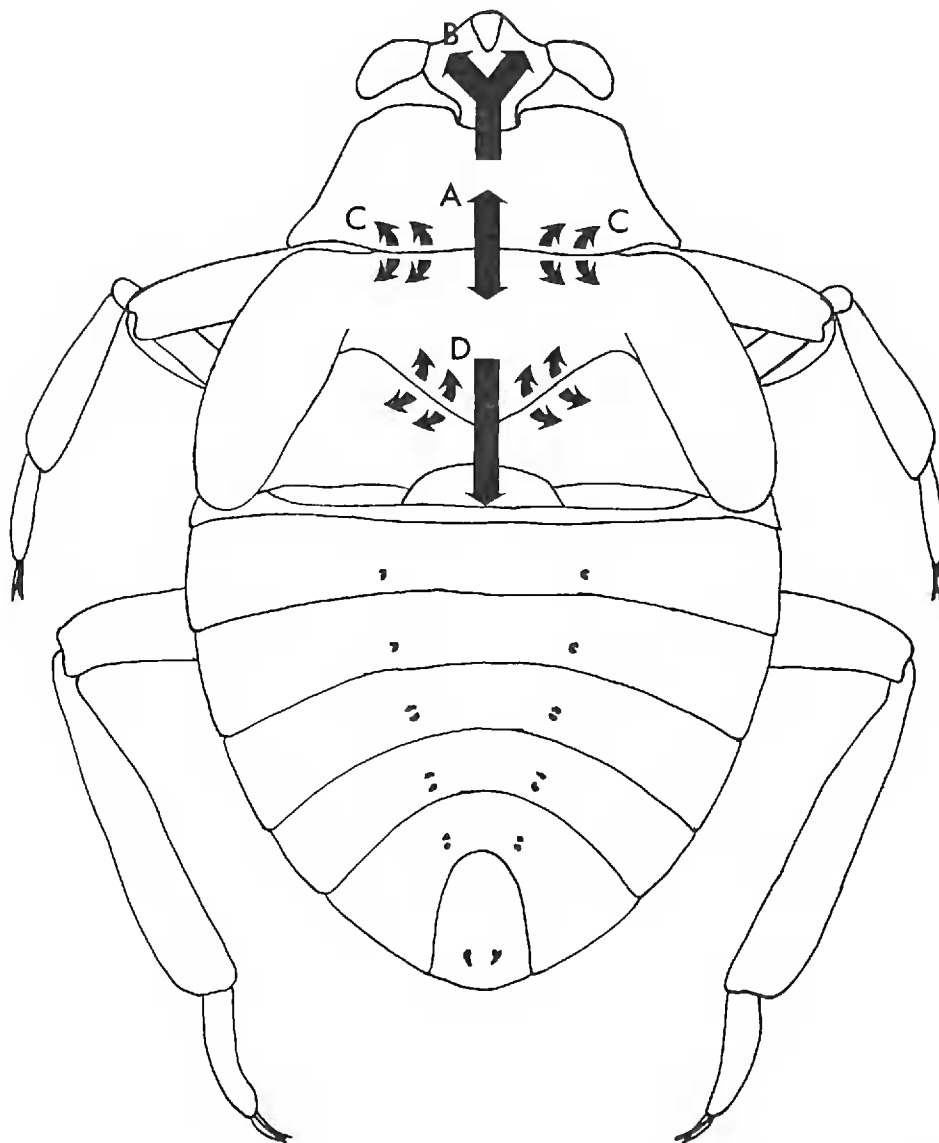


FIG. 2. Integumentary rupture sequence. A: Rupture from pro- and mesotergum. B: Elongation into coronal and frontal sutures of head. C: Spreading of meso- and metatergal sutures. D: Elongation of middorsal split through metathorax into scutellum, and spreading of metatergal, first abdominal-tergal suture.

lasting from one to 20 minutes, is apparently governed by the bug's ability to secure oxygen in this way.)

Once the old cuticle is shed, the freshly emerged second through fifth instar nymphs can again obtain atmospheric oxygen via the abdominal air store. A newly emerged adult theoretically has two ways of getting oxygen: first, via the subalar air store, and second, via the ventral abdominal air store. My observations suggest that adults favor the former method. If this is the case, it would be advantageous for the emerging adult to have its wings expanded and hemelytra interlocked to provide the subalar store as soon as possible after leaving the last nymphal skin. As Figure 1 illustrates, the subalar air

storage system is available to the adult as soon as it is clear of the old skin. The bug must surface to provision the system with air.

AN EXPERIMENT

A first instar and two third instar nymphs were denied access to the surface of the water at the onset of their molting, after each had gripped its middle legs as shown in Figure 1B, G. This was accomplished by means of a fiberglass screen wire disc which displaced the molting individuals below the surface. In all three cases, molting proceeded as previously described to the point at which an emerging nymph or adult would normally rest (Fig. 1E). Under the experimental conditions, nymphs did not rest, but rapidly abandoned their skins and began wild swimming under the plastic screen. When the screen was removed, each of the three nymphs immediately went to the surface, assumed the air acquisition position, and remained there for from two to ten minutes. These results suggest that surface contact is not essential during the actual shedding process, but that the resting period that follows depends on access to atmospheric air through the cast skin.

DISCUSSION

An adaptation to meet the respiratory requirements of molting nymphs may have occurred early in the shift of the Hydrocorisae from littoral to truly aquatic habitats (see China 1955, and Lauck and Menke 1961 for phylogeny). Certain problems accompanied the "need" to molt on the water's surface, not the least of which are weightlessness and lack of a holding substrate. Anyone who has attempted to shed his clothing while floating free in water will better appreciate the difficulty of this feat. *Abedus herberti* seems to have solved these problems by establishing an allostatic basis when it clasps its middle legs with its raptorial front legs. The resulting pressure and leverage obtained by this behavior seem essential to the molting process, and the ability to perform the behavior was probably a necessary preadaptation to surface molting. What nonmolting behavioral patterns of belostomatids and of nepids suggest that such a preadaptation did in fact exist? Grooming. Both nepids and belostomatids retain the ability to groom their middle legs with their front legs even though the forelegs are directed anteriorly and are highly specialized for grasping prey. The grooming pattern differs from the molting in that the middle legs are groomed separately but clasped simultaneously at the onset of shedding.

Emerging adults belonging to several hemimetabolous orders (Odonata, Homoptera, Orthoptera, and other Hemiptera) characteristically

do not begin inflating their wings until free from the nymphal skin. Apparently the subalar air storage system is sufficiently important for belostomatids that selection has favored a system whereby wing inflation is accomplished during the molting process. Since nepids also employ a subalar air store as adults (Parsons 1973), I suspect they possess this adaptation as well. Studies on the molting behavior of representatives of all groups of the Hydrocorisae are needed to establish the origin of both surface molting and early wing inflation.

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SCIENTIFIC NOTE

Biological Observations on *Tropidishia xanthostoma* Scudder (Orthoptera: Gryllacrididae).—*Tropidishia xanthostoma* Scudder is an obscure troglophile of the subfamily Rhabdophorinae in the monogeneric tribe Tropidishiini occurring only on the Pacific Slope. S. H. Scudder (1861, Proc. Bost. Soc. Nat. Hist., 8: 6-14 and 1862, Bost. Journ. Nat. Hist., 7(3): 409-480) and A. N. Caudell (1916, Proc. U.S. Nat. Mus., 49: 655-690) describe taxa. This note offers biological observations on the cricket. Additional observations have been offered by Buckell (1922, Proc. Ent. Soc. Br. Col., 20: 9-41 and 1930, Proc. Ent. Soc. Br. Col., 27: 17-51) and Fulton (1928, Ent. News, 39: 8).

My observations were made from January to November, 1973, at an abandoned mine near Mill City, Oregon, in a coniferous forest type biome. The *Tropidishia* population and other troglophilic fauna occurred inside the mine within 70m of the entrance.

T. xanthostoma nymphs of body size to 5mm exhibit conspicuous coloration being light tan to cream color having antennae, thorax, abdomen, metathoracic femora, and tibiae mottled or banded dark brown as characteristic of uniformly colored adults. Maculation disappears through early instar development yielding uniform dark amber coloration which slightly darkens into rich brown at maturity. Antennae and tibiae remain banded through development.

Strong white or red light or sound in the mine does not appear to affect the crickets. Antennae are generally very active and the insects exhibit remarkable agility. Individuals were never noted on the mine floor or in ponded water in the mine tunnels.

Several nymphs were observed in spider webs near the mine entrance but no predation on specimens was observed. No specimens were observed in surrounding subterranean and epigean habitats either at night, during the day, or during crepuscular periods. A pit-fall trap line deployed in August, October, and November failed to capture any *Tropidishia* specimens.

Ecdysis in *Tropidishia* is similar to the process in other insects beginning with symmetrical splitting of the ventral notum. Spent exoskeletal tissue peels from the emerging insect. Coloration of the new instar darkens slightly after emergence and the insect, characteristic of other cavernicoles, consumes the exuvium.

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